The role of urban habitats in the abundance of red squirrels (Sciurus vulgaris, L.) in Finland

Jokimäki, Jukka

2017-10

Jokimäki , J , Selonen , V , Lehikoinen , A & Kaisanlahti-Jokimäki , M-L 2017 , ' The role of urban habitats in the abundance of red squirrels (Sciurus vulgaris, L.) in Finland ' , Urban Forestry & Urban Greening , vol. 27 , pp. 100-108 . https://doi.org/10.1016/j.ufug.2017.06.021

http://hdl.handle.net/10138/307392
https://doi.org/10.1016/j.ufug.2017.06.021

The role of urban habitats in the abundance of red squirrels (*Sciurus vulgaris*, L.) in Finland

Highlights

- The winter abundance of red squirrels is higher in urban than in forest habitats.
- Spruce crop size increase squirrel abundance.
- Feeding sites (+) and cats (-) affect squirrel abundance.
- Urban environments are an important alternative habitat for the declining red squirrel in Europe.
- The urbanization of squirrels can be monitored using citizen science based, large-scale winter surveys.

Abstract

Because the amount of urban areas has increased, it is important to investigate the abundance of wildlife species in relation to urban environments. Analyzing the impact of urbanization on the presence of forest-dwelling mammals is of interest due to the possible effects of urbanization on human-wildlife relationships and urban biodiversity. The Eurasian red squirrel (*Sciurus vulgaris*) is a declining forest species, and its occurrence in urban environments has been inadequately studied. The loss and fragmentation of forests due to urbanization may be detrimental for squirrels, whereas the abundant and predictable food resources and the low number of natural predators in urban areas may encourage squirrels to invade towns. We used large-scale data collected by volunteer bird watchers along a 950 km south-north gradient to study whether the winter abundance of squirrels in Finland is dependent on urbanization, while controlling for

effects of habitat type, food abundance (spruce cone crop; number of winter feeding sites), predator abundance (northern goshawk, *Accipiter gentilis*; feral cat *Felis catus*), season and latitude. We found that squirrel abundance increased with human population density, number of feeding sites and spruce cone crop and decreased with latitude and season. Feral cats showed weak negative connection with squirrel numbers, but there were no effect of goshawks. Relative squirrel abundance was approximately twice as high in urban habitats than in forests. Artificial feeding rather than a low number of predators may attract squirrels in urban environments. Planting spruce trees in urban environments will also benefit squirrels. Our results indicate that urban areas are an important habitat for the red squirrel even along the northern edge of their distribution range, where natural forest areas are still widespread. We conclude also that a citizen science -based bird survey protocol associated with mammal surveys seems to be a good large-scale monitoring method to study the urbanization of squirrels.

Keywords: winter feeding; mammals; monitoring; predation; urbanization, citizen science

1. Introduction

Globally, more people now live in urban than in rural areas, and at the same time, urbanized areas are increasing at an even higher rate than the urban population (UN, 2014). According to Seto et al. (2011), global urban land cover will increase approximately 30-fold by 2030. Therefore, understanding the impact of urban development on animal populations is important due to the possible effects on biodiversity and human-wildlife relationships (Baker and Harris, 2007; Bateman and Fleming, 2012). Urbanization is one of the most extreme forms of land-use alteration, and only remnants of the original habitats persist in towns. At the same time, urban

47 areas are characterized by high levels of predictable anthropogenic food resources and human-
48 caused disturbances (e.g., traffic), milder microclimates, and an altered abundance of predators
49 (e.g., Rebele, 1994; Shochat et al., 2006; Gilbert, 2012; Francis and Chadwick, 2013;
50 Tryjanowski et al., 2015).
51
52 Urbanization is globally recognized as one of the main threats to biodiversity (Wilcox and
53 Murphy, 1985). An important challenge for urban ecology is to conserve species that live in
54 urban environments. In addition, most of the contacts between people and nature occur in urban
55 environments, and citizen views related to conservation are formed in urban environments
56 (Lepczyk and Warren, 2012; Shanahan et al., 2014). Urban mammals have been used by urban
57 inhabitants for aesthetic, biological and recreational purposes (Adams, 2016). Unfortunately,
58 mammalian diversity generally decreases with urbanization (McCleery, 2010). However, the
59 behavioral flexibility of individuals and increased human tolerance might favor the urbanization
60 of some species (Baker and Harris, 2007; McCleery, 2010; Lowry et al., 2012).
61
62 Natural environments that are modified by human activities possess challenges to native animals.
63 During recent decades, many new mammalian species, such as the European red fox (*Vulpes*
64 *vulpes*, L.; Francis and Chadwick, 2012), raccoon (*Procyon lotor*, L.; Adams, 2016), and
65 Eurasian badger (*Meles meles*, L.; Harris, 1984) have colonized urban areas. Some of them (e.g.,
66 the red fox) currently have even higher densities in urban areas than in their natural habitats
67 (Bateman and Fleming, 2012). However, only a few mammal species, such as the brown rat
68 (*Rattus norvegicus*, Berkenhaut) and the house mouse (*Mus musculus*, L.), are abundant in town
69 centers (Gilbert, 2012).

Urban areas have some features, such as stable and abundant food resources and low numbers of natural predators that may attract wildlife and promote, for example, the urbanization of squirrels (Francis and Chadwick, 2013; Adams, 2016). Artificial feeding stations and waste offer easily available food resources, especially to species feeding on seeds or having a generalist diet (Adams, 2016). Although feeders in gardens are primarily designed to feed birds, they also attract squirrels in urban areas, especially during the winter when food resources may become scarce in forest habitats. In general, urban areas contain a lower number of larger natural predators than do rural areas (Bateman and Fleming, 2012), but the abundance of medium-sized carnivores might be even higher in urban environments than in more natural environments (Nilon and Pais, 1997; Baker and Harris, 2007; Bateman and Fleming, 2012). However, at the same time, urban squirrels may be more vulnerable to predation by domestic cats than are squirrels living in rural and forest areas (Wauter et al., 1997; Shuttleworth, 2001; Magris and Gurnell, 2002). It is likely that there is an optimal level of human influence at which the living requirements for a species are best met or limit the level of urbanization that a species can tolerate (Francis and Chadwick, 2013; Adams, 2016). However, the roles of artificial food and the number of predators promoting the urbanization of squirrels are still not well known.

Arboreal squirrels (*Sciurus* spp.) are strictly dependent on forests. Therefore, they might be sensitive to the forest loss caused by urbanization. However, urban areas also contain different types of green spaces, such as remnant habitat patches, cemeteries, public parks and the gardens of residential areas, which may be suitable living environments for many forest species (Adams, 2016). For example, squirrels can also inhabit fragments of forests within the urban matrix (Veerboom and Abeldorf, 1990; Baker and Harris, 2007; Babińska-Werka and Żółw, 2008;

93 Parker and Nilon, 2012; Mäkeläinen et al., 2015; Fey et al., 2016). The red squirrel (*Sciurus*
94 *vulgaris*, L.) is a native forest specialist species in most European countries, and although the
95 species still is common throughout most of its range (Gurnell and Wauters, 1999), its current
96 population is declining in many parts of Europe (Gurnell and Pepper, 1993; O 'Teangana et al.,
97 2000; Bertolino and Genovesi, 2003; Shar et al., 2008; Selonen et al., 2010). Most previous red
98 squirrel studies were conducted within forest or agricultural areas and considered the effects of
99 fragmentation on the red squirrel at a relatively small local scale. These studies indicated that red
100 squirrel occurrence and abundance increase with woodland size (Celada et al., 1994; Verbeylen
101 et al., 2003) and the area of woodland covered by coniferous trees (Veerboom and Abeldorf,
102 1990) but decrease with the distance from the nearest source area (Veerboom and Abeldorf,
103 1990; Celada et al., 1994; Verbeylen et al., 2003).
104
105 Only a few red squirrel studies have been conducted within urban areas despite the fact that the
106 species is currently quite common in urban habitats in Europe (Luniak, 2004; Babińska-Werka
107 and Żółw, 2008). One local study conducted in Brussels indicated that patch size and patch
108 quality have positive effects and that isolation has a negative effect on red squirrel patch
109 occurrence in urban areas (Verbylen et al., 2003). A study in Warsaw parks also indicated that
110 park size positively affects red squirrel abundance (Babinska-Werka and Zolow, 2008).
111 However, large-scale studies with multiple study sites and covering different habitats are needed
112 to better understand the urbanization process of red squirrel. In addition, as squirrels are
113 important dispersal agents of seeds (Steele, 2008), they may also impact on distribution of urban
114 trees. Therefore, it is important to know how urbanization influence squirrel abundance.
115

The main aim of this study was to analyze how human density affects the winter abundance of red squirrels throughout Finland. The analysis included also habitat type, natural (size of the Norway spruce cone crop) or artificial (number of feeding sites) food abundance, and natural (northern goshawk, *Accipiter gentilis,* L.) or human-associated (feral cats, *Felis domesticus*, L.) predator abundance. In addition, we also studied whether latitude and the time of the winter season affect the squirrel abundance. We conducted our study during the winter season because winter is a critical period for the survival of squirrels in the northern latitudes (Selonen et al. 2015), and because due to the lack of leaves in the broad-leaved trees, the detectability of squirrels is high during winter (Hernández, 2014). We predicted that if squirrels somehow benefit from humans, then their abundance should increase with human density and should be higher within urban than other habitat types. If food resources, either artificial or natural, have an effect then squirrel abundance should increase with the number of feeding sites or with the size of the Norway spruce cone crop. If squirrel winter abundance is dependent on predators, then their abundance should change with predator abundance. Because the severity of winter increases toward the north, we predicted that red squirrel abundance would decrease from the south to the north. Due to winter mortality, we predicted that squirrel abundance would decrease during the winter. However, the squirrel abundance could also increase towards to the spring, because the visibility of squirrels increases due their early-starting mating season.

2. Methods

2.1. Study area

139

140 The study was conducted in Finland along an approximately 950 km south-north gradient
141 (Appendix 1; between 59°50' and 68°40' N and 19°40' and 30°20' E). The human population of
142 Finland was 5.5 million in 2014 with a mean population density of 18/km^2 (Statistics Finland,
143 2015). The majority of the human population is concentrated in the southern part of the country
144 (approximately 170 inhabitants/km^2), whereas the population density is the lowest in the north
145 (approximately 0.2 inhabitants/km^2; Statistic Finland, 2015). Approximately 78% of the total
146 area of Finland (390,906 km²) is land covered (Statistics Finland, 2015), and approximately 77%
147 of this is forests, 9% is agricultural areas and only 4% is built-up areas. Almost the entire country
148 belongs to the boreal taiga forest terrestrial biome, where forests are dominated by coniferous
149 trees. The study area lies within the cool boreal climate zone.
150

151 The study was conducted during the winter season. The average monthly temperature during
152 mid-winter in December 2014 (study year) was -1.3°C (1981–2010 long-term average -3.2°C) in
153 southern Finland (Helsinki) and -8.4°C (-11.7°C) in northern Finland (Sodankylä; Finnish
154 Meteorological Institute, 2014). The corresponding amounts of snow cover on the 15th of
155 December were 4 cm (1981–2010 long-term average 6 cm) in Helsinki and 32 cm (1981–2010
156 long-term average 36 cm) in Sodankylä. The coniferous tree cone crop, the primary food of the
157 squirrels, was moderate during the studied winter (Finnish Museum of Natural History, hereafter
158 FMNH).

159 *2.2. Study species*

160 The red squirrel occupies the boreal and temperate areas of Eurasia and is mainly a coniferous
161 forest specialist (Shar et al., 2008). Individuals live in the same home ranges throughout the year,

although they may move between habitats depending on the food situation (Wauters and Dhondt, 1992). In Finland, urban squirrels were first observed in the southern part of the country in the cities of Helsinki and Turku in the early 1930s (Haapanen, 1999).

The main natural food of the red squirrel is seeds of coniferous trees; in Finland, these are mainly Norway spruce seeds (*Picea abies*, Karst) (Helle, 1996; Selonen et al., 2015). The main predator of the red squirrel in Finland is the northern goshawk (Selonen et al., 2010, Sulkava et al., 2014). In some other countries, red foxes and feral cats are also important squirrel predators (Loss et al., 2013).

2.3. Field data and sampling

Earlier mammal survey monitoring in Finland has been based on wildlife transect route and triangle surveys conducted outside urban environments and coordinated by the Finnish Game and Fisheries Institute (currently the Natural Resources Institute Finland; Lindén et al., 1996). Due to the restrictions of the triangle surveys (no data from urban areas), we used data collected by bird watchers during the Finnish winter bird surveys (Koskimies and Väisänen, 1991). A similar approach combining avian and mammal surveys has also been used in the UK (Battersby et al., 2004). Since the winter of 2014/2015, the number of mammals (individuals/10 km transect route) has also been counted during the Finnish winter bird surveys.

The Finnish winter bird surveys consist of transect routes with an average length of approximately 10 km (Koskimies and Väisänen, 1991). Birds and mammals are surveyed along the same transect route three times per winter: early winter (1–15 November), mid-winter (25

December to 7 January) and late winter (21 February to 6 March). The yearly surveys are organized by the FMNH and are conducted by volunteer birders (610 during the studied winter of 2014/2015). The participants can identify all winter birds and their calls. Thus, the observers are skilled in species identification, and since the red squirrel is very easy to identify, there should not be any differences between observers in ability to identify the target species of this study.

The location of a transect route is selected freely by the volunteers, but the coordinator of the surveys, the FMNH, ensures that the transect routes do not overlap. In this study, 355 transect routes (279 surveyed during the early winter, 279 surveyed during the mid-winter and 258 surveyed during the late winter) with a total of 7,789 transect route kilometers (2,651 early winter km, 2,669 mid-winter km and 2,469 late winter km) were surveyed during the winter of 2014/2015. The spatial distribution of the mid-winter (25 December to 7 January) survey transect routes is shown in Appendix 1. The transect route is counted by walking during midday under good weather and light conditions. When counting, the counter walks slowly, stops and listens, and records observation notes. The survey cannot last longer than the duration of daylight in mid-winter, that is, for example, approximately 4 hours in northern Finland. At each route the survey time is kept about the same in all three survey periods. Note that no vehicles are used in the surveys. The proportion of each habitat type along the route is estimated in advance from the maps and air photos, and ground-checked in the field during the surveys. When the route runs along a border of two habitats, the length is halved between them. Habitats along the route are classified into eight categories within an accuracy of 100 meters: (a) dumping ground or fur farm (data in this study: 11 km of transect routes); b) urban settlement (construction zones, town

centers, private homes with gardens, urban parks, etc.; 2003 km); c) rural settlement (widely dispersed buildings within agricultural landscapes; 1233 km); d) arable land (897 km); e) forest (2812 km); f) clear-cut area or stand of saplings (262 km); g) reed bed or shore scrub (150 km); and h) other (including also over-flying individuals; 421 km). Thus, the distribution of transect routes is somewhat concentrated near human settlements, but the sample size outside these areas is also substantial (e.g., >2800 km in forests). All observed squirrels, northern goshawks and feral cats (either seen or heard at an unlimited distance; note that no snow tracks are included in the data) are placed in one of the eight habitat categories in the field. For example, one route may consist 8000 meters of urban and 2000 meters of forest habitat including four squirrels observed in urban and one squirrel in forest habitat type. The observers also count the number of winter feeding sites in each of the above-mentioned habitats and estimate the size of the Norway spruce cone crop in trees along the transect routes during the each survey (six cone abundance categories; from 1 = no cones to 6 = very abundant cone availability; note that only the fresh cones are used to do this estimation). Because the methods do not allow density estimates, an index of relative abundance (individuals/10 km transect route) is used in this study. A more detailed description of the survey protocol is given elsewhere (see Koskimies and Väisänen, 1991, Lehikoinen et al., 2013; Fraixedas et al., 2015).

2.4. Human densities

The human densities (inhabitants/km^2) around the survey transect routes were estimated using the coordinates of the transect route and the human density register of Statistics Finland provided by the IT Center of Science (https://sui.csc.fi/applications/paituli(PalTuli/index-html). We placed a rectangle around the survey transect route based on the southernmost, northernmost, easternmost and westernmost location of the transect route. Based on the human density register, we estimated how many people live inside this rectangle and used it as a proxy for the human density around the survey transect route. This work was conducted using the ArcMap 10.3.1 software (Redlands, California, USA).

2.5. Statistical analyses

We conducted analyses at two scales. In the first analysis, we investigated which factors influence transect route-specific squirrel numbers at the large landscape level using transect route-specific variable values. In the second analysis, we used more detailed data within the transect routes to investigate the habitat selection of squirrels using habitat-specific transect route sections. The first analysis was only possible using 285 routes where the exact location of the route was available and we were thus possible to calculate the human densities around the route. In the second analyses all 355 routes were included.

First, we evaluated the transect route-specific values of squirrel number using generalized mixed effect models, where the transect route-specific number of observed squirrels was explained using the length of the transect route, the survey season (categorical variable), the latitude and longitude of the transect route, the linear and quadratic effects of human density (log

253 transformed), and the abundance of winter feeding sites (log transformed) and predators
254 (goshawks and feral cats). The length of the transect route accounts for the fact that the lengths
255 of the transects vary between routes. The quadratic effect of human density accounts for the
256 possibility that squirrel numbers can experience, e.g., a peak or drop in areas of average human
257 density. We also included an interaction term between latitude and human density as well as
258 human density and abundance of feeding sites in the analyses. These can take into account that
259 impact of human density can depend on latitude and feeding may affect squirrel numbers
260 differently in areas of high and low human densities. The transect route ID was used as a random
261 factor because most of the transect routes were surveyed during all three winter sub-seasons.
262 Length of the route, coordinates and census season were included in all the models, but
263 otherwise we used all model combinations of used variables. Altogether, this produced 56
264 different model combinations. The length of the transect route (continuous variable), latitude
265 (continuous variable), longitude (continuous variable) and survey season (categorical factor
266 variable) were included in all models and thus formed the base model. The numbers of predators
267 (goshawks and cats) and winter feeding sites were transformed into relative abundances (number
268 of animals or feeders per 10 survey kilometer).
269
270 Second, we investigated the habitat-specific values of squirrel numbers using generalized mixed
271 effect models. For this analysis, we split the transect routes into sections based on eight different
272 habitat categories (see section 2.3. Field data). Habitat was used as eight categorical factor
273 variable and forest habitat was used as a reference category. In this analysis, the squirrel numbers
274 were explained by the length of the transect route section (continuous variable), habitat type of
275 this transect route section, survey season (categorical factor variable), latitude of the transect

route (continuous variable), abundance of winter feeding sites in the transect route section (continuous variable) and relative abundance of spruce cones along the full transect route (continuous variable). Like in the first analysis, the ID of the transect route was used as a random factor in the analysis. The length of the transect route section, latitude and census season were included in all models and thus formed the base model. In this analysis, the habitat-specific squirrel abundance was compared to that in the forested areas. In addition, we tested whether detection probability might be season dependent between natural and urban areas by adding an interaction between season and habitat. Altogether, we built 9 different model combinations.

Both analyses were conducted using the stepwise procedure. First, using the full model, we measured which distribution models, (i) Poisson, (ii) zero-inflated Poisson, (iii) negative binomial or (iv) zero-inflated negative binomial distribution, best fit the data. Second, among these four alternatives, we used the best of the top-ranked distributions in the full set of candidate models. We used the Akaike information criterion (AIC hereafter) to perform model selection (Burnham and Anderson, 2002).

All analyses were conducted in R version 3.2.2 (R Development Core Team, 2013) and models were fitted using glmmadmb-package. When analyzing spatial data, it is possible that autocorrelation of variables may bias the results. The potential spatial autocorrelation of residuals of the best model was investigated by using the ncf-package in R. No spatial autocorrelation was found from the residuals of the best models. Also multicollinearity among explanatory variables may have confounding effects on results. In our case, there was no strong correlation between the explanatory variables. The maximum Pearson's correlation coefficient

299 was always below 0.5 (Booth et al. 1994), except in the case of human densities and quadratic
300 effect of human densities. In this case only one of these two variables were used at time.

301

302 **3. Results**

303

304 Altogether, 1781 squirrels were observed along the transect routes across all seasons (early
305 winter 785, mid-winter 448, late winter 548). The relative squirrel abundance, feeding sites,
306 goshawks and cats in the different habitats are shown in Table 1. In general, the relative squirrel
307 abundance was lower in forest (1.43 individuals/10 km transect route) than in rural (4.00
308 individuals/10 km transect route) or urban (4.24 individuals/10 km transect route) habitats. In
309 addition, the number of feeding sites per 10 km transect route was lower in forest (0.72) than in
310 rural (19.46) or urban (18.26) habitats. The relative abundance of northern goshawks in urban
311 areas (0.57 individuals/10 km transect route) was approximately twice as high as in forest (0.27)
312 or rural (0.22) habitats. Approximately twice the number of feral cats was observed in rural (0.66
313 individuals/10 km transect route) than in urban habitats (0.30), whereas only one cat was
314 observed in the forest habitats (Table 1).

315

316 In the transect route analyses, the zero-inflated negative binomial models were top-ranked in the
317 first model selection step (results not shown). In the second step of the transect route-specific
318 analysis, the top-ranked model included the length of the transect route, latitude, longitude,
319 season, abundance of feral cats, quadratic effect of human density and abundance of feeding
320 places and their interaction. The other model within 2 ΔAIC of the best model included these

same variables, but also interaction between quadratic human density and latitude (Table 2). However, since this interaction was not significant this variable can be considered as uninformative parameter (sensu Arnold 2010) and only the top ranked model was investigated later on. The number of squirrels increased with the increasing length of a transect route, quadratic effect of human density (Fig. 1a) and abundance of feeding sites (Fig 1b) and decreased with increasing latitude (Table 3). The significant negative interaction between quadratic human population and abundance of feeding sites suggest that feeding increased squirrel numbers more in areas where there was lower human densities (Table 3). There was also tendency that abundance of feral cats decreased squirrel numbers (Table 3). The relative squirrel abundance was significantly lower during the mid-winter and late winter counts than the early winter counts. The abundances of goshawks was not significantly associated with squirrel numbers (Table 2).

In the habitat-specific analyses, the negative binomial models were top-ranked in the first model selection step (results not shown). In the second step of the habitat-specific analysis, the full model was clearly the best model (Table 4). This top-ranked model included the length of the transect route, latitude, season, habitat, number of feeding sites and spruce cone crop. Based on the top-ranked model coefficients, transect route length, most habitat types, abundances of feeders and the size of the Norway spruce cone crop and seasons differed significantly from zero (Table 5). The highest abundances were observed in urban and rural settlements, where the relative squirrel abundances (approximately 4 squirrels per 10 km transect route) were significantly higher than those in forests (approximately 2 squirrels per 10 km transect route) or other habitats (0-1 squirrels per 10 km transect route; Fig. 2a). In contrast, the relative abundance

344 of red squirrels in arable land and reed beds was significantly lower than that in forests (Fig. 2a,
345 Table 5). In addition, the relative squirrel abundance increased with increasing transect length,
346 number of feeders and number of spruce cones (Table 5; Fig. 2b). As in the transect route-
347 specific analysis, the relative squirrel abundance decreased from early winter to the mid-winter
348 and late winter (Table 5).
349

350 **4. Discussion**

351

352 Our analysis indicated that red squirrel abundance increased with human density. The
353 relationship between squirrel abundance and human density was nonlinear, as squirrel abundance
354 increased more rapidly in areas with the highest human densities. Our habitat-specific analysis
355 further showed that the squirrel abundance was significantly higher in urban and rural
356 settlements than in other habitats, such as forests. These results suggest that the wintering red
357 squirrels benefits from urbanization.
358

359 We found a higher red squirrel abundance in urban and rural settlements than in forest habitats.
360 Red squirrels inhabited urban habitats similarly in different parts of Finland, as indicated by the
361 non-significant interaction term between latitude and human density. Therefore, the urbanization
362 of the red squirrel in Finland appears to be in a phase in which no geographical difference in the
363 level of urbanization can be seen. It has been concluded that the spread of urbanization in
364 different geographical regions depends on whether urbanization in different cities occurs
365 independently or through the migration of urbanized individuals from one city to another (Evans
366 et al., 2009, 2010, Fey et al., 2015). In the case of the red squirrel in Finland, the process of how

different cities have become urbanized remains unknown, but it is known that the arrival of squirrels to urban areas began in the southwestern cities of Finland approximately 90 years ago (Haapanen, 1999). The population dynamics of urbanized squirrels remain unclear in our study. However, the squirrels abundances observed in this study should reflect the local population size, because dispersal distances of red squirrels are short, usually 1-2 km, although occasionally even 10-20 km moved distances can be observed (Selonen and Hanski, 2015). In other words, squirrels in our study areas likely do not make migrations between urban and rural areas (Selonen & Hanski 2015, Fey et al. 2016) but the abundances observed here reflect the local population size. In Warsaw, Poland, it is observed that red squirrel abundance has increased threefold from 1956 to 2000 in the urban areas (Babinska-Werka and Zolow, 2008). In our study, squirrel abundance decreased toward the north (both in rural and urban habitats), a trend that could be expected because the productivity of forests declines and winter harshness increases toward the north.

Squirrel abundance was greatest in areas with the highest human population density. Because we evaluated human density at a relatively coarse scale, we cannot compare squirrel abundance, for example, between town centers and suburban areas. In general, the amount of woodlands decreases with increasing human density, but parks with trees are common in Finland, even in town centers. Red squirrels may survive quite well within these urban areas (Fey et al., 2016). However, it is fair to suppose that squirrel abundance is higher in suburban areas than in more urbanized areas because winter feeding is more common in these residential private-house areas than in urban core areas (Väisänen, 1999).

389 One factor related to the high squirrel abundance observed in urban areas could be winter
390 feeding. Our study indicated that squirrel abundance increased with the number of winter feeding
391 sites. Many mammal species living in urban areas use feeding sites. According to the results of
392 the Finnish winter feeding site study program 1988/89-1998/99, almost all (about 40) Finnish
393 winter-active mammal species are detected in the feeding sites (n = 455 sites), and the red
394 squirrel is the most common mammalian species occurring at 71% of these sites (Väisänen,
395 1999). Our results indirectly indicated that squirrels are more able to utilize feeding sites in areas
396 with a lower human density. Therefore, putting artificial feeders in natural areas may be a good
397 management option. Supplemental food provided by humans is one possible reason why
398 squirrels have urbanized. Likely because of artificial feeding, escape distances of squirrels have
399 declined, and they have become tame (Luniak, 2004; Parker, and Nilon, 2012; Uchida et al.,
400 2015). In addition, behavioral flexibility may be one reason for the success of some mammal
401 species, such as squirrels, in urban environments (Bateman and Fleming, 2014).
402
403 Previous studies have indicated that winter feeding may be beneficial, e.g., for the grey squirrel
404 (e.g., Bonnington et al., 2014). Winter feeding and anthropogenic waste offer great and
405 predictable food resources for animals, especially during the winter period and years when the
406 main food sources of squirrels, i.e., the seeds of conifers, are scarce. For example, Verbeylen et
407 al. (2003) found that patches with supplementary feeding had a higher probability of being
408 occupied by the red squirrel. Winter feeding has apparently helped squirrels adjust to urban and
409 suburban habitats. Feeding wildlife is widespread and have a many impacts on the wildlife
410 (Orams, 2002). While many previous studies have suggested artificial feeding have positive
411 effects especially on birds (Siriwardena et al., 2007; Harrison et al., 2009), some other papers

412 have also indicated its risk (Jones et al., 2008). Currently, negative aspects of supplemental
413 feeding have been actively discussed in urban areas (Galbraith et al., 2015), for instance, animals
414 aggregated by artificial feeding could be more vulnerable to pathogen transmission (Bradley, and
415 Altizer 2006). Also, the possibility of ecological traps may be worth to consider (Robertson et
416 al., 2013; Hanmer et al., 2017). However, there are also psychological benefits of the wildlife for
417 the humans, enhanced by artificial feeding (Orams, 2002).
418
419 Our results indicated that squirrel abundance increased with the spruce cone crop. This is not a
420 surprising result since spruce seeds are main food for the red squirrel (Gurnell and Wauters,
421 1999; Selonen et al., 2015). Favoring spruce trees will likely increase the living possibilities of
422 squirrels in urban environments. We note that our study year had a moderate spruce cone crop;
423 thus, crop failure did not push animals to feeders in urban areas. Bowers and Breland (1996) and
424 Petty et al. (2003) also indicated that food availability (either artificial food or conifer seeds) is
425 the main factor limiting the number of tree squirrels. However, because previous studies have
426 indicated that the squirrel numbers in winter follow spruce cone production in Finland (Selonen
427 et al., 2015), multi-year surveys are needed to study the role of artificial feeding for squirrels in a
428 more detailed way. For example, it may be that feeding sites are even more important for
429 squirrels during poor cone years than during those years with average cone production, as in our
430 case. However, Reher et al. (2016) found that food provision in semi-urban habitat had positive
431 effect on red squirrels also in years when natural food sources were available. One factor that
432 might promote the urbanization of squirrels is the so- called “urban heat island” phenomenon
433 (Adams, 2016). Animals living in warmer conditions may survive with less energy than

434 individuals occupying in colder environments. Unfortunately, we had no data to analyze this
435 topic, but it might be a relevant topic for further study.
436
437 Earlier studies have suggested that predator presence, but not food supplementation, affects red
438 squirrel abundances in forest habitats during winter (Selonen et al., 2016). Some studies have
439 indicated that urban areas have few predators, which may support the urbanization of some
440 species (Bateman and Fleming, 2012). However, in our case, the main squirrel predator in our
441 areas, the goshawk, was more abundant in human-dominated areas than in forest habitats. This
442 result is affect by the fact that many goshawks (especially juveniles) migrate to cities in winter in
443 Finland. In any case, urban environments can no longer be considered predator-free areas for red
444 squirrels. Similar to our study, other studies have also indicated that predators, either natural or
445 human-associated, have no role in relative squirrel abundance (Bateman and Breland, 1996;
446 Petty et al. 2003). Our results indicate that amount of feral cats can limit squirrel numbers. Also
447 many earlier studies have indicated the harmful impact of the non-native cat predation on native
448 animal fauna in general (Moseby et al., 2015; Adams, 2016) and also on squirrels (Baker et al.,
449 2005). Limiting cat numbers could help squirrel populations in urban and rural areas.
450
451 We must stress that we were not able to control for the detectability of squirrels in different
452 seasons (Hernández, 2014) and habitats (see e.g. Amori et al., 2011), and this may have partly
453 affected our results. For example, detectability of squirrels has been reported to be higher in late
454 autumn and winter than summer or spring because dense foliage decreased the detectability of
455 squirrels during summer (Hernández, 2014). We detected the lowest relative squirrel abundance
456 during the mid-winter, indicating an increase towards the end of winter. Towards to early-spring

(i.e. late winter season in our case) day length becomes longer and the activity of squires would also increase partly due to mating activities. The detectability of the red squirrel may be either higher in human-dominated habitats than in more natural habitats due to the attraction to artificial feeders, less hiding places (e.g. tree cavities, dense woods) or changing individual personalities (bolder in urban habitat; Lowry et al., 2013), or the detectability of squirrels may also be low in urban environments because buildings decrease detectability of squirrels (our personal observations). However, the detectability of squirrels may be higher in open rural areas than in more closed forest and urban habitats, which may partly explain the high squirrel abundance in the rural landscape. In any case, supporting our results, previous studies have indicated that squirrel densities are lower in rural than in urban environments (Babińska-Werka and Żółw, 2008; Dozières et al., 2012). In addition, we tested whether detection probability might be season dependent in urban areas compared to more natural areas, by testing the effect of interaction between season and human population size. This interaction was not significant.

We used mammalian data collected by the volunteer bird watchers during their winter bird surveys. This citizen science-based survey and monitoring method has several benefits. First, the winter bird transect routes also cover urban environments, which are lacking in Finnish wildlife monitoring efforts. Second, a large number of bird watchers can collect mammalian data from large areas. The use of volunteer-based annual monitoring enables the production of long-term datasets of the distribution and population trends of many mammalian species (Battersby and Greenwood, 2004). In addition, winter surveys are a good method for monitoring squirrel abundance because squirrels are easiest to detect in winter (Babińska-Werka and Żółw, 2008).

5. Conclusions

Our results indicate that the level of urbanization is high among European red squirrel populations (Verbeylen et al., 2003, Babińska-Werka and Żółw, 2008; Dozières et al., 2012; Rézouki et al., 2014). Based on our data, red squirrels use urban areas even along the northern edge of their distribution range, where natural forest areas are still widespread. During winter, more red squirrels were detected in urban than in forest habitats. In the light of observations that red squirrels in forests and rural areas are declining in many European countries (Shar, 2008; Selonen et al., 2010), urbanized areas may provide an important alternative habitat for the red squirrel. Consequences of urban development are not always disadvantages for native species. Our study indicated that human presence may have positive effect on red squirrels, for example winter feeding sites attract squirrels within urban environments and thereafter offer more wildlife contact for urbanites and suburbanites. Increasing amount of spruce trees in urban environments will increase food resources and offer hiding places for the squirrels. Citizen science has become more and more popular for ecological and evolutionary studies (e.g. Newman et al., 2003; Silvertown, 2009), unfortunately very few studies have been conducted in mammals. Our study show how citizen science data can be used for monitoring mammal species in urban areas.

Acknowledgements

We thank all of the volunteers who participated in this nationwide survey; without their help, this large-scale work would not have been possible. AL was funded by the Academy of Finland (grant 275606). Ministry of Environment has supported winter bird censuses in Finland. The language usage in this article was checked by the Wiley Editing Service.

References

Adams, C.E., 2016. Urban Wildlife Management. 3rd Edition, Taylor and Francis, New York.

Amori, G., Mortelliti, A., Guidarelli, G., Schiavano, A., Luiselli, L. 2012. Detectability of the European red squirrel (Sciurus vulgaris) in a Mediterranean area. Rendiconti Lincei, 23, 203-206.

Arnold, T. W., 2010: Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74: 1175–1178.

Babińska-Werka, J. and Żółw, M (2008). Urban populations of the red squirrel (Sciurus vulgaris) in Warsaw. Annales Zoologici Fennici 45, 270-276.

Baker, P. J., Bentley, A. J., Ansell, R. J.,Harris, S. 2005. Impact of predation by domestic cats Felis catus in an urban area. Mammal Review, 35, 302-312.

Backer, P.J., Harris, S., 2007. Urban mammals: what does the future hold? An analysis of the factors affecting patterns of use of residential gardens in Great Britain. Mammal Review 37, 297-315.

Bateman, P. W., Fleming, P.A., 2012. Big city life: carnivores in urban environments. Journal of Zoology 287, 1-23.

Bateman, P.W., Fleming, P.A., 2014. Does human pedestrian behaviour influence risk assessment in a successful mammal urban adapter? Journal of Zoology 294, 93-98.

Battersby, J E., Greenwood, J.J., 2004. Monitoring terrestrial mammals in the UK: past, present and future, using lessons from the bird world. Mammal Review 34, 3-29.

Becker, D. J., Streicker, D. G., Altizer, S., 2015. Linking anthropogenic resources to wildlife–pathogen dynamics: a review and meta-analysis. Ecology Letters, 18, 483-495.

Bertolino, S., Genovesi, P., 2003. Spread and attempted eradication of the grey squirrel (Sciurus carolinensis) in Italy, and consequences for the red squirrel (Sciurus vulgaris) in Eurasia. Biological Conservation 109, 351-358.

Bonnington, C., Gaston, K.J., Evans, K.L., 2014. Squirrels in suburbia: influence of urbanisation on the occurrence and distribution of a common exotic mammal. Urban Ecosystems 17, 533-546.

Booth, G., Niccolucci, M., Schuster, E, 1994. Identifying proxy sets in multiple linear regression: an aid to better coefficient interpretation. U.S. Department of Agriculture Forest Service, Washington, D.C.

Bowers, M., Breland, B., 1996. Foraging of gray squirrels on an urban-rural gradient: use of the GUD to assess anthropogenic impact. Ecological Applications 6, 1135–1142.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference. Springer, New York.

Celada, C., Bogliani, G., Gariboldi, A.,Maracci, A., 1994. Occupancy of isolated woodlots by the red squirrel Sciurus vulgaris L. in Italy. Biological Conservation 69, 177-183.

Dozières. A., Chapuis. J.-L., Thibault. S., Baudry. E., 2012. Genetic structure of the French red squirrel populations: implication for conservation. PloS ONE 7: e47607. doi: 10.1371/journal.pone.0047607

Evans, K.L., Gaston, K.J., Frantz, A.C., Simeoni, M., Sharp, S.P., McGowan, A., Dawson, D.A., Walasz, K., Partecke, J., Burke, T., Hatchwell, B. J., 2009. Independent colonization of multiple urban centres by a formerly forest specialist bird species. Proceedings of the Royal Society B-Biological Sciences 276**,** 2403-2410.

Evans, K.L., Hatchwell, B.J., Parnell, M., Gaston, K. J.,2010. A conceptual framework for the colonisation of urban areas: the blackbird Turdus merula as a case study. Biological Reviews 85**,** 643-667.
Fey, K, Hämäläinen, S, Selonen, V., 2016. Roads are no barrier for dispersing red squirrels in an urban environment. Behavioral Ecology 27, 741-747.
Fey, K., Vuorisalo, T., Lehikoinen, A., Selonen V., 2015. Urbanization of the wood pigeon (Columba palumbus) in Finland. Landscape and Urban Planning 134, 188-194.
Finnish Meteorological Insitute, 2014. Climate Statistics Finland 2014 and 2015. Helsinki.
Forman, R.T., Alexander, L.E., 1998. Roads and their major ecological effects. Annual review of ecology and systematics 29, 207-231,
Fraixedas Nuñez, S., Lehikoinen, A., Lindén, A., 2015. Impact of climate and land change on wintering bird populations in Finland. Journal of Avian Biology 46, 63–72.
Francis, R.A., Chadwick, M.A., 2012. What makes a species synurbic. Applied Geography 32, 1200-1216.
Francis, R.A., Chadwick, M.A., 2013. Urban ecosystems: understanding the human environment. Routledge, Cornwall.
Galbraith, J. A., Beggs, J. R., Jones, D. N., Stanley, M. C., 2015. Supplementary feeding restructures urban bird communities. Proceedings of the National Academy of Sciences, 112(20), E2648-E2657.
Gilbert, O., 2012. The ecology of urban habitats. Springer Science and Business Media.
Gurnell, L.J., Pepper, H., 1993. A critical look at conserving the British red squirrel Sciurus vulgaris. Mammal Review 23, 127-137.
Gurnell, J., Wauters, L., 1999. Sciurus vulgaris. In: A. J. Mitchell-Jones, G. Amori, W. Bogdanowicz,, B., Kryštufek, P.J.H., Reijnders, F., Spitzenberger, M., Stubbe, J. B.M., Thissen, V., Vohralík, J., Zima (Eds), The Atlas of European Mammals (180-181). Academic Press, London.
Haapanen, E., 1999. Menneisyyden Helsingin eläimet: pääkaupungin nisäkkäät, matelijat ja sammakkoeläimet arkistolähteissä vuosina 1850–1980. Helsingin kaupungin ympäristökeskuksen julkaisuja. 4. (in Finnish)
Hanmer, H. J., Thomas, R. L., Fellowes, M. D. 2017. Provision of supplementary food for wild birds may increase the risk of local nest predation. Ibis, 159, 158-167.
Harris, S., 1984. Ecology of urban badgers Meles meles: distribution in Britain and habitat selection, persecution, food and damage in the City of Bristol. Biological Conservation 28, 349-375.
Harrison, T. J., Smith, J. A., Martin, G. R., Chamberlain, D. E., Bearhop, S., Robb, G. N., Reynolds, S. J., 2010. Does food supplementation really enhance productivity of breeding birds?. Oecologia, 164, 311-320.
Helle, P., 1996. Orava. In: Lindén, H., M. Hario., Wikman, M. (Eds.), Riistan jäljille. Oy Edita Ab, Helsinki, pp. 26-29. (in Finnish)
Hernández, Á., 2014. Seasonal habitat use in Eurasian red squirrels residing in Iberian hedgerows. Hystrix, the Italian Journal of Mammalogy, 25, 95-100.
Jones, D. N., James Reynolds, S., 2008. Feeding birds in our towns and cities: a global research opportunity. Journal of Avian Biology, 39, 265-271.
Koskimies, P.,Väisänen, R.A., 1991. Monitoring Bird Populations - A Manual of Methods Applied in Finland. - Zoological Museum, Finnish Museum of Natural History, University of Helsinki, Helsinki. Available at: http://www.luomus.fi/en/methods-bird-monitoring

Lehikoinen, A., Lehikoinen, E., Valkama, J., Väisänen, R. A., Isomursu, M., 2013. Effects of Trichomonas-epidemics on Finnish greenfinch and chaffinch populations. Ibis 155, 357–366.
Lepczyk, C.A., Warren, P.S. (Eds.), 2012. Urban bird ecology and conservation (Vol. 45). University of California Press, London
Lindén, H., Hario, M., Wikman, M., (Eds.), 1996. Riistan jäljille. Oy Edita Ab, Helsinki. (in Finnish)
Loss, S. R., Will, T., Marra, P.P., 2013. The impact of free-ranging domestic cats on wildlife of the United States. Nature communications 4, 1396.
Lowry, H., Lill, A., Wong, B., 2013. Behavioural responses of wildlife to urban environments. Biological Reviews 88, 537-549.
Luniak, M., 2004. Synurbanization—adaptation of animal wildlife to urban development. In: Shaw, WW, LK Harris, Vandruff, L. (Eds.), Proceedings of the 4 th International Urban Wildlife Symposium. University of Arizona. Tucson, Arizona, pp. 50-55.
Magris, L., Gurnell, J., 2002. Population ecology of the red squirrel (Sciurus vulgaris) in a fragmented woodland ecosystem on the Island of Jersey, Channel Islands. Journal of Zoology 256, 99-112.
Moseby, K. E., Peacock, D. E., Read, J. L. 2015. Catastrophic cat predation: a call for predator profiling in wildlife protection programs. Biological Conservation, 191, 331-340.
Mäkeläinen, S., Schrader, M.,Hanski, I.K., 2015. Factors explaining the occurrence of the Siberian flying squirrel in urban forest landscape. Urban Ecosystems 18, 223-238.
McCleerly, R., 2010. Urban Mammals. In: Aitkenhead, J.,Volder, A. (Eds.), Urban Ecosystem Ecoloogy, Agronomy Monographs 55. American Society of Agronomy, Crop Science of America, Soil Science of America, Madison. pp. 87-102.
Newman, G., Wiggins, A., Crall, A., Graham, E., Newman, S., Crowston, K., 2012. The future of citizen science: emerging technologies and shifting paradigms. Frontiers in Ecology and the Environment, 10, 298-304.
Nilon C.H., Pais, R.C., 1997 Terrestrial vertebrates in urban ecosystems: developing hypotheses for the Gwynns Falls Watershed in Baltimore, Maryland. Urban Ecosystems 1, 247–57.
Orams, M. B., 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. Tourism management, 23, 281-293.
O´Teangana, D.O., Reilly, S., Montgomery, W I., Rochford, J., 2000. Distribution and status of the red squirrel (Sciurus vulgaris) and grey squirrel (Sciurus carolinensis) in Ireland. Mammal Review 30, 45-56.
Parker, T.S., Nilon, C.H., 2012. Urban landscape characteristics correlated with the synurbization of wildlife. Landscape and Urban Planning 106, 316-325.
Petty, S.J., Lurz, P.W.W., Rushton, S.P., 2003. Predation of red squirrels by northern goshawks in a conifer forest in northern England: can this limit squirrel numbers and create a conservation dilemma? Biological Conservation 111, 105–114.
R Development Core Team, 2013. R: A language and environment for statistical computing. Version 3.2.2.
Rebele, F., 1994. Urban ecology and special features of urban ecosystems. Global ecology and biogeography letters 4, 173-187.
Reher, S., Dausmann, K. H., Warnecke, L., Turner, J. M. (2016). Food availability affects habitat use of Eurasian red squirrels (Sciurus vulgaris) in a semi-urban environment. Journal of Mammalogy, gyw105.

Rézouki, C., Dozières, A., Le Cœur, C., Thibault, S., Pisanu, B., Chapuis, J.L., Baudry, E., 2014. A Viable Population of the European Red Squirrel in an Urban Park. PloS one, 9(8), e105111. doi: 10.1371/journal.pone.0105111.
Robertson, B. A., Rehage, J. S., Sih, A., 2013. Ecological novelty and the emergence of evolutionary traps. Trends in Ecology & Evolution, 28, 552-560.
Selonen, V., Sulkava, P., Sulkava, R., Sulkava, S., Korpimäki, E., 2010. Decline of flying and red squirrels in boreal forests revealed by long-term diet analyses of avian predators. Animal Conservation 13, 579-585.
Selonen, V., Hanski, I.K., 2015. Occurrence and dispersal of the red squirrel and the Siberian flying squirrel in fragmented landscapes. In: Shuttleworth, C. M., Lurz, P. W., Hayward, M. W., Red Squirrels: ecology, conservation and management in Europe. European Squirrel Initiative. Woodbridge Google Scholar, pp.67-82.
Selonen V, Varjonen R, Korpimäki E., 2015. Immediate or lagged responses of a red squirrel population to pulsed resources. Oecologia 177, 401–411.
Selonen, V., Varjonen, R., Korpimäki, E., 2016. Predator presence, but not food supplementation, affects forest red squirrels in winter. Annales Zoologici Fennici, 53, 183-193.
Seto, K.C., Fragkian, M., Güneralp, B., Reuilly, K.M., 2011. A meta-analysis of global urban land expansions. Ploss One, 6,:e23777.
Shanahan, D.F., Strohbach, M.W., Warren, P.S., Fuller, R.A., 2014. The challenges of urban living. In: Gil, D., Brumm, H. (Eds), Avian Urban Ecology. Oxford University Press, Oxford, pp. 3-20.
Shar, S., Lkhagvasuren, D., Bertolino, S., Henttonen, H., Kryštufek, B., Meinig, H., 2008. Sciurus vulgaris. The IUCN Red List of Threatened Species 2008: e.T20025A9135609. http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T20025A9135609.en. Downloaded on 28 January 2016.
Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E., Hope, D., 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in ecology and evolution 21, 186-191.
Shuttleworth, C.M., 2001. Traffic related mortality in a red squirrel (Sciurus vulgaris) population receiving supplemental feeding. Urban Ecosystems 5, 109-118.
Silvertown, J., 2009. A new dawn for citizen science. Trends in Ecology & Evolution, 24, 467-471.
Siriwardena, G. M., Stevens, D. K., Anderson, G. Q., Vickery, J. A., Calbrade, N. A., Dodd, S. 2007. The effect of supplementary winter seed food on breeding populations of farmland birds: evidence from two large-scale experiments. Journal of Applied Ecology, 44, 920-932.
Statistics Finland, 2015. Statistical Yearbook of Finland 2014. Helsinki.
Steele, M.A., 2008. Evolutionary interactions between tree squirrels and trees: A review and synthesis. Current Science 95, 871-876.
Sulkava, S., Lokki, H., Solonen, T., 2014. Kanahaukan pesimäaikainen ravinto kaupunkiympäristössä ja maaseudulla Etelä-Suomessa (Diet of the Northern Goshawk during the breeding season in urban and rural environments in Southern Finland). Suomen Riista 60, 20-30. (In Finnish, with English summary)
Tryjanowski, P., Skórka, P., Sparks, T.H., Biaduń, W., Brauze, T., Hetmański, T., Kawa, P., 2015. Urban and rural habitats differ in number and type of bird feeders and in bird species

consuming supplementary food. Environmental Science and Pollution Research 22, 15097-15103.
Uchida, K., Suzuki, K., Shimamoto, T., Yanagawa, H., Koizumi, I., 2015. Seasonal variation of flight initiation distance in Eurasian red squirrels in urban versus rural habitat. Journal of Zoology 298, 225-231.
Väisänen, R.A., 1999.Talvilintujen ruokintapaikoilla vierailevat petolinnut ja nisäkkäät (Occurrence of raptors, owls and mammals at feeding sites of winter birds in Finland). Linnut 34, 8–11. (in Finnish, with English summary)
Verboom B., van Apeldoorn R., 1990. Effects of habitat fragmentation on the red squirrel, Sciurus vulgaris L. Landscape Ecology 4, 171–176.
Verbeylen, G., De Bruyn, L., Adriaensen, F., Matthysen, E., 2003. Does matrix resistance influence Red squirrel (Sciurus vulgaris L. 1758) distribution in an urban landscape? Landscape ecology 18, 791-805.
UN, 2014. World urbanization prospects, the 2014 revision. Department of economic and social affairs, population division, New York.
Wauters, L. A., Somers, L., Dhondt, A., 1997. Settlement behaviour and population dynamics of reintroduced red squirrels Sciurus vulgaris in a park in Antwerp, Belgium. Biological Conservation 82, 101-107.
Wauters, L., Dhondt, A.A., 1992. Spacing behaviour of red squirrels, Sciurus vulgaris: variation between habitats and the sexes. Animal Behaviour 43, 297-311.
Wilcox, B.A., Murphy, D.D., 1985. Conservation strategy: the effects of fragmentation on extinction. The American Naturalist 125, 879-887.

Appendix 1. Relative abundances of red squirrels at Finnish survey sites (black circles; larger circles indicate higher abundances). X markings show sites where the species was not observed in counts. The red circles show the locations of the 20 largest cities in Finland.

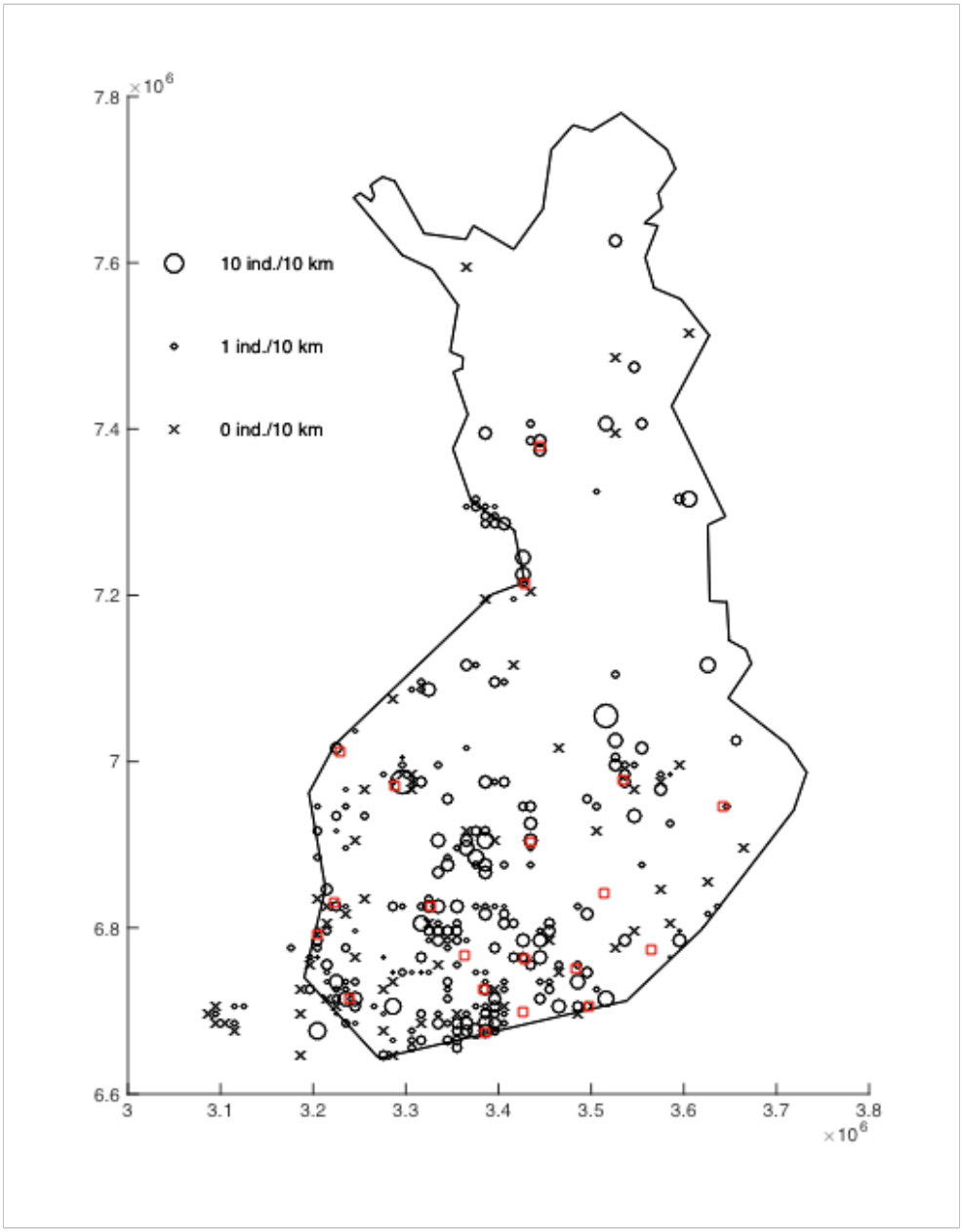
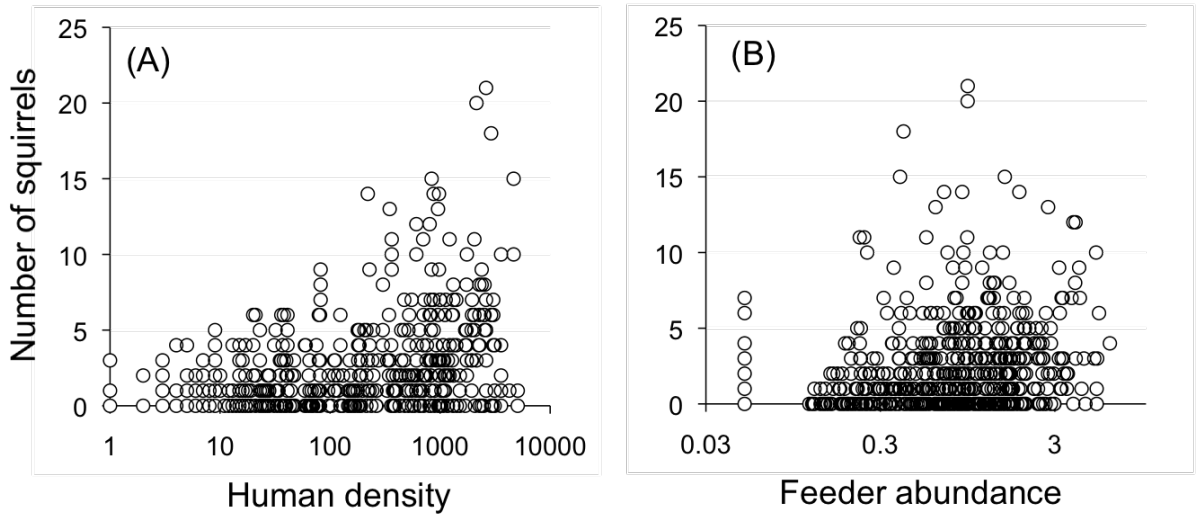

×10^6
7.8
7.6
7.4
7.2
7
6.8
6.6
10 ind./10 km
1 ind./10 km
0 ind./10 km
3
3.1
3.2
3.3
3.4
3.5
3.6
3.7
3.8
×10^6

Figure legends:

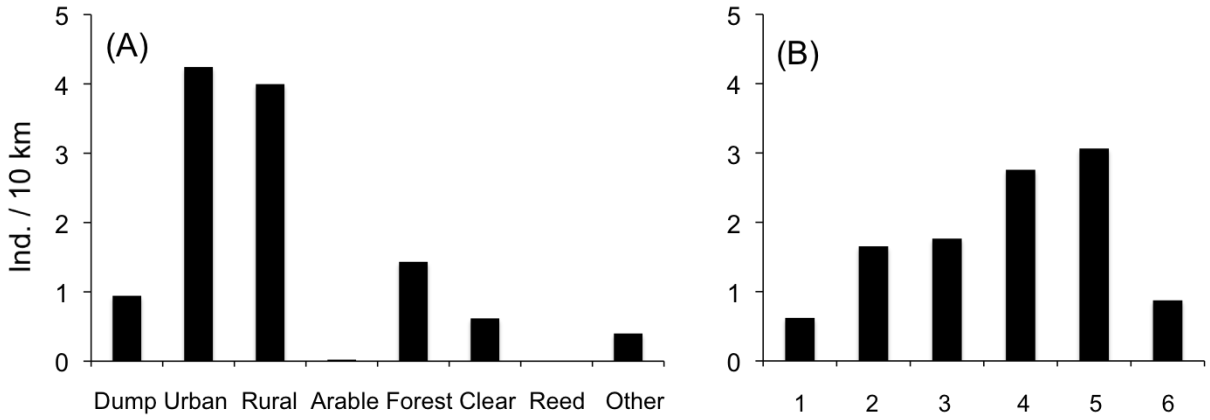
Fig. 1. Relative squirrel abundance per transect route in relation to (A) human density (humans/km²) and (B) abundance of feeding sites (feeding sites/transect route km). Note the log scale of the x-axis.

Fig 2. Relative abundances of red squirrels (individuals per 10 km survey transect route) in relation to (A) different habitat types (dumping grounds, urban and rural areas, arable land, forest (trees > 5 m), clear-cut areas and stands of saplings (trees < 5 m), reed beds, shore scrub, and others), and (B) different spruce cone crop levels (1 = none, 2 = very few, 3 = few, 4 = moderate, 5 = abundant, 6 = very abundant (only three transect routes of these).



Jokimäki et al. Fig. 1.

Fig. 1. Relative squirrel abundance per transect route in relation to (A) human density (humans/km²) and (B) abundance of feeding sites (feeding sites/transect route km). Note the log scale of the x-axis.



Jokimäki et al. Fig 2.

Fig 2. Relative abundances of red squirrels (individuals per 10 km survey transect route) in relation to (A) different habitat types (dumping grounds, urban and rural areas, arable land, forest (trees > 5 m), clear-cut areas and stands of saplings (trees < 5 m), reed beds, shore scrub, and others), and (B) different spruce cone crop levels (1 = none, 2 = very few, 3 = few, 4 = moderate, 5 = abundant, 6 = very abundant (only three transect routes of these).

Table 1. Relative squirrel abundance and number feeding sites in different habitats (and their lengths) surveyed during winter bird counts.

	Squirrels	Feeders	Goshawks	Cats	Kilometers
Forest	403	203	75	1	2812
Dump-land	1	4	2	0	11
Urban	850	3657	115	69	2003
Rural	493	2399	28	81	1233
Arable land	2	23	26	2	897
Clear-cut	26	54	1	0	421
Reed-bed	0	4	7	0	262
Other	6	9	67	29	150

Table 2. Models explaining the transect route-specific abundance of squirrels in Finnish winter surveys, ranked based on the AIC. The AIC difference (ΔAIC), AIC weight (w) and evidence ratio (E-rat) are shown. Transect route ID was used as a random factor in all models. Length is the length of the transect route. Lat and Lon are the latitude and longitude of the transect route, respectively. Season is the survey season. H and H2 are the log-transformed human density and its quadratic effect along the transect route, respectively. Hawk, Cat and Feed are the abundances of goshawks, cats and feeding sites, respectively.

Model	ΔAIC	w	E-ratio
Length+Lat+Lon+Season+H2*F+Cat	0.00	0.27	1.00
Length+Lat+Lon+Season+H2*Lat+Cat+H2*F	1.82	0.11	2.48
Length+Lat+Lon+Season+H2*F+Hawk+Cat	2.00	0.10	2.72
Length+Lat+Lon+Season+H2*F	2.12	0.09	2.89
Length+Lat+Lon+Season+Cat+H2+F	2.98	0.06	4.44
Length+Lat+Lon+Season+Cat+H2	3.82	0.04	6.75
Length+Lat+Lon+Season+H2*Lat+Hawk+Cat+H2*F	3.82	0.04	6.75
Length+Lat+Lon+Season+H2*Lat+H2*F	3.94	0.04	7.17
Length+Lat+Lon+Season+H2*F+Hawk	4.12	0.03	7.85
Length+Lat+Lon+Season+H2*Lat+Cat+F	4.60	0.03	9.97
Length+Lat+Lon+Season+H*F+Cat	4.68	0.03	10.38
Length+Lat+Lon+Season+H2+F	4.86	0.02	11.36
Length+Lat+Lon+Season+Hawk+Cat+H2+F	4.96	0.02	11.94
Length+Lat+Lon+Season+H+Cat+F	5.80	0.01	18.17
Length+Lat+Lon+Season+H2*Lat+Hawk+H2*F	5.94	0.01	19.49

Length+Lat+Lon+Season+H2*Lat+F	6.50	0.01	25.79
Length+Lat+Lon+Season+H*Lat+Cat+H*F	6.56	0.01	26.58
Length+Lat+Lon+Season+H2*Lat+Hawk+Cat+F	6.58	0.01	26.84
Length+Lat+Lon+Season+H*F	6.62	0.01	27.39
Length+Lat+Lon+Season+H*F+Hawk+Cat	6.64	0.01	27.66
Length+Lat+Lon+Season+Hawk+H2+F	6.84	0.01	30.57
Length+Lat+Lon+Season+H*Lat+Cat+F	7.50	0.01	42.52
Length+Lat+Lon+Season+H+F	7.56	0.01	43.82
Length+Lat+Lon+Season+H+Hawk+Cat+F	7.80	0.01	49.40
Length+Lat+Lon+Season+H2*Lat+Hawk+F	8.48	0.00	69.41
Length+Lat+Lon+Season+H*Lat+H*F	8.50	0.00	70.11
Length+Lat+Lon+Season+H*Lat+Hawk+Cat+H*F	8.52	0.00	70.81
Length+Lat+Lon+Season+H*F+Hawk	8.56	0.00	72.24
Length+Lat+Lon+Season+H*Lat+F	9.28	0.00	103.54
Length+Lat+Lon+Season+H+Hawk+F	9.54	0.00	117.92
Length+Lat+Lon+Season+H*Lat+Hawk+H*F	10.46	0.00	186.79

Length+Lat+Lon+Season+H	49.08	0.00	>10000
Length+Lat+Lon+Season+H+Cat	49.42	0.00	>10000
Length+Lat+Lon+Season+H*Lat	50.84	0.00	>10000
Length+Lat+Lon+Season+H+Hawk	51.08	0.00	>10000
Length+Lat+Lon+Season+H*Lat+Cat	51.16	0.00	>10000
Length+Lat+Lon+Season+H+Hawk+Cat	51.42	0.00	>10000
Length+Lat+Lon+Season+H*Lat+Hawk	52.84	0.00	>10000
Length+Lat+Lon+Season+H*Lat+Hawk	52.84	0.00	>10000
Length+Lat+Lon+Season+H*Lat+Hawk+Cat	53.16	0.00	>10000
Length+Lat+Lon+Season+H*Lat+Hawk+Cat	53.16	0.00	>10000
Length+Lat+Lon+Season+H2	53.80	0.00	>10000
Length+Lat+Lon+Season+H2*Lat	55.44	0.00	>10000
Length+Lat+Lon+Season+Hawk+H2	55.80	0.00	>10000
Length+Lat+Lon+Season+H2*Lat+Cat	55.86	0.00	>10000
Length+Lat+Lon+Season+Hawk+Cat+H2	56.24	0.00	>10000
Length+Lat+Lon+Season+H2*Lat+Hawk	57.42	0.00	>10000

Length+Lat+Lon+Season+H2*Lat+Hawk+Cat	57.84	0.00	>10000
Length+Lat+Lon+Season+Cat+F	70.62	0.00	>10000
Length+Lat+Lon+Season+F	71.14	0.00	>10000
Length+Lat+Lon+Season+Hawk+Cat+F	71.68	0.00	>10000
Length+Lat+Lon+Season+Hawk+F	72.14	0.00	>10000
Length+Lat+Lon+Season	142.04	0.00	>10000
Length+Lat+Lon+Season+Cat	143.18	0.00	>10000
Length+Lat+Lon+Season+Hawk	143.20	0.00	>10000
Length+Lat+Lon+Season+Hawk+Cat	144.36	0.00	>10000

Table 3. Parameter estimates and test values for variables explaining the transect route-specific abundances of red squirrels in Finland in winter surveys based on the top-ranked model. Coefficients that differ significantly from zero are bolded and nearly significant values ($P < 0.1$) are show in *italic*.

Variable	B ± SE	z	P
Intercept	**4.884 ± 2.215**	**2.21**	**0.0274**
Length	**0.043 ± 0.016**	**2.66**	**0.0078**
Latitude	**-0.008 ± 0.003**	**-3.01**	**0.0026**
Longitude	0.002 ± 0.005	0.39	0.6986
Season, mid-winter	**-0.931 ± 0.089**	**-10.48**	**< 0.0001**
Season, late-winter	**-0.637 ± 0.003**	**-7.48**	**< 0.0001**
Human density^2	**0.023 ± 0.003**	**7.36**	**< 0.0001**
Feeding places	**0.662 ± 0.111**	**5.97**	**< 0.0001**
Cat	*-2.253 ± 1.161*	*-1.94*	*0.0522*
Human density^2*Feeding places	**-0.006 ± 0.003**	**-2.18**	**0.0290**

Table 4. Models explaining habitat-specific abundances of squirrels in Finnish winter surveys, ranked based on the AIC. AIC difference (ΔAIC), AIC weight (w) and evidence ratio (E-rat) are shown. Transect route was used as a random factor in all models. Length is the length of the transect route section. Lat is the latitude of the transect route. Season is the survey season. Hab is the habitat category of the transect route section. Feed is the abundance of feeders in the transect route section. Spruce is the transect route-specific spruce cone crop abundance.

Model	ΔAIC	w	E-rat
Length+Lat+Season+Hab+Feed+Spruce	0	0.997	1
Length+Lat+Season+Hab+Feed	11.90	0.003	363.8
Length+Lat+Season*Hab+Feed+Spruce	17.98	0	8022.5
Length+Lat+Season+Hab+Spruce	35.96	0	>10000
Length+Lat+Season+Hab	49.06	0	>10000
Length+Lat+Season+Feed+Spruce	612.52	0	>10000
Length+Lat+Season+Feed	621.50	0	>10000
Length+Lat+Season+Spruce	827.24	0	>10000
Length+Lat+Season	840.38	0	>10000

Table 5. Parameter estimates and test values for variables explaining the section-specific squirrel abundances in Finland based on the top-ranked model. Coefficients that differ significantly from zero are bolded.

Variable	B	SE	Z-value	P
Intercept	-0.56	1.65	-0.34	0.735
Length (per 100m)	**0.01**	**0.00**	**6.70**	**< 0.001**
Dumpland	-0.71	1.02	-0.69	0.489
Urban settlements	**0.81**	**0.11**	**7.31**	**< 0.001**
Rural settlements	**0.50**	**0.10**	**4.95**	**< 0.001**
Arable land	**-4.37**	**0.71**	**-6.14**	**< 0.001**
Clear-cut	-18.30	11.40	-0.02	0.987
Reedbeds	**-3.37**	**0.71**	**-4.72**	**< 0.001**
Other	**-2.70**	**0.39**	**-6.98**	**< 0.001**
Feeders	**0.04**	**0.01**	**6.25**	**< 0.001**
Spruce cones	**0.17**	**0.04**	**3.75**	**< 0.001**
Season, mid-winter	**-0.65**	**0.08**	**-7.79**	**< 0.001**
Season, late-winter	**-0.41**	**0.08**	**-4.97**	**< 0.001**

Latitude	-0.00	0.00	-0.58	0.562